Succession in a kelp bed ecosystem ; clearing of primary substrate by wave-induced kelp sweeping

Kelp ecosystem
Sweeping range
Succession
Expansion
Repair mechanisms

Écosystèmes à laminaires
Rayon de balayage
Succession
Expansion
Mécanismes de reconstitution

Branko Velimirov
Zoologisches Institut der Universität Wien, Abteilung für Meeresbiologie, Althanstr. 14, 1090 Wien, Austria.

ABSTRACT

Observing that wave induced sweeping of the fronds of plants at the edges of kelp patches results in a relatively barren interface between kelp plants and the surrounding animal patches led to the assumption that : *a*) kelp sweeping could provide protection for macrophytes from grazers; and *b*) that it could be a mechanism allowing kelp patch expansion. The validity of the hypothesis was supported by quantitative observations on the sweeping capabilities of individual kelp plants and by characteristic species/biomass distributions within the kelp sweeping zone, the kelp patches and the adjacent animal patches. In addition, experimental clearing of the primary substrate within the various areas showed that free space will be completely occupied within 50 days unless kelp sweeping stops the faunal progression. A model describing the mechanisms that bring about successional changes at the edge of a kelp patch and leading to its expansion is proposed. The importance of kelp sweeping as a mechanism for expansion of small patches and as a repair mechanism for large patches after storm induced destruction of the edges, is discussed.

Oceanol. Acta, **1983**. Proceedings 17th European Marine Biology Symposium, Brest, France, 27 September-1 October, 1982, 201-206.

RÉSUMÉ

Succession dans un écosystème à laminaires; dégagement des frondes du substrat primaire par le balayage sous l'effet de la houle

A la périphérie des « ilôts » de laminaires (« kelp »), les frondes mises en mouvement par les vagues balayent le substrat. Ceci donne naissance à une zone marginale dépourvue d'organismes entre les laminaires et les peuplements animaux. Cette observation permet d'avancer les hypothèses suivantes :

a) le balayage des frondes protège celles-ci de la prédation par les brouteurs ;

b) le balayage est un mécanisme de croissance de la communauté permettant l'extension des taches de laminaires.

Ces hypothèses sont étayées par les observations quantitatives sur les capacités de balayage par les frondes, ainsi que par les distributions caractéristiques des espèces et de leur biomasse dans les différentes zones. De plus, des expériences de dépeuplement des laminaires montrent que le substrat est totalement repeuplé en 50 jours, à moins que le balayage ne stoppe cette progression de la faune avoisinante.

Un modèle décrivant les phénomènes qui occasionnent les changements dans la succession à la périphérie des « ilôts » de laminaires et permettent leur extension, est proposé. L'importance du balayage en tant que mécanisme d'extension pour les « ilôts » de petite taille et comme mécanisme de restauration pour les larges « ilôts » après tempête est discutée.

Oceanol. Acta, **1983**. Actes 17e Symposium Européen de Biologie Marine, Brest, 27 septembre-1er octobre 1982, 201-206.

INTRODUCTION

Most of our knowledge about the development of ecological systems is based on long term observation about changes in composition, number and biomass of the component species of the community, and such patterns are generally termed successions. Additionally, a great number of studies, concerned with interactions within ecosystems on the species level (Dayton, 1971; Connel, 1972; Paine, 1974) as well as on the community level (Fishelson, 1977; Ott, Fedra, 1977; Ott, 1981) indicate that there is more to succession than changes in assemblages or associations of populations.

As pointed out by Odum (1969) a succession entails an interacting complex of processes, some of which counteract one another.

Although objections have been raised concerning the proposed definitions of succession and the theory of the causes of successions (Clements, 1916; Odum, 1969; Connell, 1972; Connell, Slatyer, 1977; Horn, 1975) it is generally agreed that the experimental elucidation of the functional role of major community components needs emphasis. Observations on succession and the mechanisms which produce the sequence of species were made during a distribution survey of the kelp beds off the west coast of the Cape Peninsula (South Africa). There was (Velimirov *et al.*, 1977; Velimirov, Griffiths, 1979) an overall decrease in standing crop and density of *Laminaria pallida* with increasing depth, whereas maximum biomass values of the macrophyte/m^2 remain constant throughout all depth ranges. In the deeper zones (13-20 m) there was a higher proportion of kelp free rock surface as well as a tendency towards patchiness.

In a preliminary report (Velimirov, Griffiths, 1979) the description of such kelp patches shows that they consist of large central plants with progressively smaller individuals towards the margin and a distinct belt of bare rock or " halo " separating the kelp settlement from extensive patches of potential grazers and suspension feeding animals. Observing that wave-induced sweeping of the fronds of marginal kelp plants results in a barren interface between kelp plants and animals led to the assumption that this kelp sweeping could provide protection from grazers but it could also be a mechanism allowing kelp patch expansion.

Most of the work reported in this study to test the above hypothesis is confined to the off-shore area where only one kelp species, namely *Laminaria pallida* occurs.

MATERIAL AND METHODS

Data collection and observations were made from 1975 1979. Kelp stipes and fronds were measured with a plastic tape measure. The sweeping range of individual plants and whole kelp patches was defined as the interface of bare or almost bare rock between the densely packed animal patches and the first sporophyte or kelp holdfast encountered. For individual and freshly settled kelp plants (less than one year old) and kelp patches under 1 m diameter, width of sweeping range was measured at 3 points. For kelp patches which diameter exceeded 1 m, a width of the belt measurement was taken every 50 cm along the patch circumference.

To sample densely packed and slow-moving organisms, quadrats of 0.1 m^2 were cleared. The samples were sorted to taxa and wet weighed. Sub-samples were dried to constant mass at 60 °C. To estimate the density of large and widely scattered or fast-moving animals the belt count method (Velimirov *et al.*, 1977; Field *et al.*, 1980) was used.

Two types of clearing experiments were performed. Primary substrate within animal patches was cleared of all animals over an area of 0.9-1.2 m^2 using a metal scraper. All cleared quadrats were reinspected next day and checked for remaining organisms which were removed. To avoid development of very small or juvenile organisms which had been overlooked the first day, the rock was carefully brushed clear. Primary substrate was cleared at the edges of kelp beds by uprooting whole kelp plants to prevent sweeping of kelp fronds. The same effect was obtained by cutting fronds of all juvenile plants within a certain patch edge area and by shortening the fronds of the adult sweeping kelp by approximately 70 % of its original length.

Recolonization speed and pattern of the faunal components within the animal and kelp patches were estimated by recording changes in coverage over time.

RESULTS

Distance swept by *Laminaria pallida*

Frond and stipe growth records of several sweeping plants with comparable stipe size (Fig. 1) over a period of 7 months showed the following trend : The increase of the total plant length from 70 cm to 96 cm is followed by an increase of the sweeping radius from 57 cm to 82 cm. At this stage average stipe size is 19 cm and average frond length 77 cm. Further growth of stipe and blade is marked by a decrease of the sweeping radius to 70 cm and this is kept over the following two months although total plant size increased on average by 10 cm. Heavy waves at the end of June, in winter 1978, uprooted 5 of the 8 measured plants and of the remaining ones the fronds were eroded off to less than half of their size, so that further observations were discontinued.

However, more information on the sweeping capabilities of *L. pallida* could be obtained by plotting the sweeping range of plants with varying stipe size against total plant length. A general trend towards a decrease of the sweeping range with increasing plant length beyond 130 cm could be noted (Velimirov, in prep.). The average width of the swept boundary at the edge of the kelp patches (Fig. 2) was 50 cm and varied between 30 and 85 cm, indicating that sweeping over a greater distance than the upper range observed in the experimental plants is not to be expected. Whereas juvenile plants with very small stems sweep with high efficiency, tall plants with a total length of 2 m or more do not sweep at all.

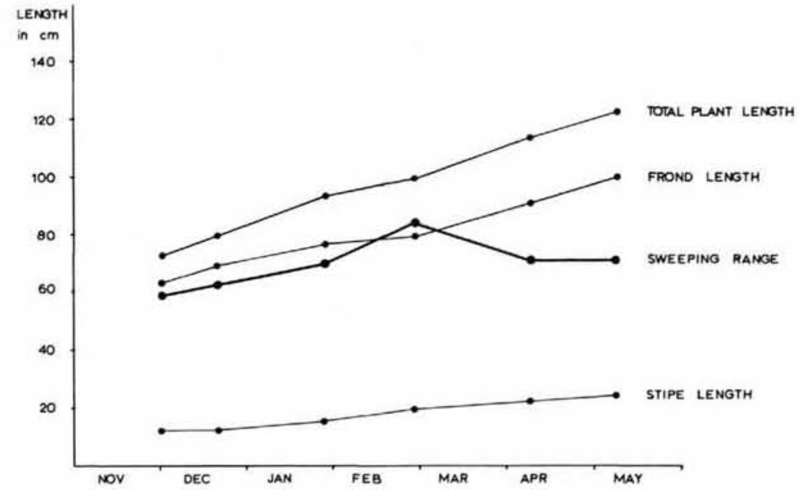

Figure 1

Changes in width of sweeping range of Lamina pallida *related to average growth of frond and stipe of 8 algae over 7 months in 1977/1978.*

Figure 2

Sweeping boundary of small kelp patch surrounded by an animal patch (Oudekraal, 13 m depth).

Effect of sweeping on the fauna

Observations on the distribution of the individual faunal components and their biomass within the kelp patches, the animal patches and the sweeping boundary are given in the Table.

Highest biomass figures were obtained from samples within animal patches and the center of the kelp patch, while extremely low figures were obtained for the sweeping zone. In contrast to the kelp patch edge, the biomass of which is nearly two orders of magnitude lower than the biomass of the kelp patch center, the faunal composition and biomass figures from the edge of the animal patch are similar to those of the patch center.

The sea cucumbers *Pentacta doliolum* and *Thyone aurea* represent the main bulk of the faunal biomass within the animal patches, followed by the ribbed mussel *Aulacomya ater* and the sea urchin *Parechinus angulosus.* A similar faunal composition and biomass can be observed within the kelp patch center. Only the ascidian *Pyura stolonifera* was never or seldom found in animal patches and *Parechinus angulosus* was less abundant than in the animal patches.

The sweeping zone is not devoid of animals but has a different and characteristic species assemblage. This area has the lowest biomass and only organisms which produce strong calcareous shells and strong attachement to the hard substrate were found, like *Aulacomya ater, Argobuccinum argus, Patella tabularis, Patella* sp., *Callochiton castaneus* and *Balanus algicola* (*see* Table), or organisms small enough to find shelter in crevices or between sedentary forms with calcareous exoskeletons.

The organisms sampled from the kelp patch edge (within 1 to 2 m behind the sweeping zone) showed no characteristic composition and could be found partly within the kelp patch as well as in the animal patch.

Recolonization of cleared areas

On average the cleared primary substrate was totally recolonized within a time period of 40 to 50 days, depending on the size of the cleared area which varied between 0.95 m^2 and 1.2 m^2.

The first organisms occupying the primary substrate were *Parechinus angulosus* and *Thais squamosa.* Their mode of feeding, namely grazing and debris feeding for *P. angulosus* and scavenging for *T. squamosa*, kept them in motion.

The main components of the animal patch assemblage, the sea-cucumbers *P. doliolum* and *T. aurea,* which

Table

Species biomass distribution in specific areas within the kelp bed. All figures are mean dry weight values per 0.1 m^2 of lo random quadrats. Figures in parenthesis are standard deviations.

Organisms	Animal patch		Sweeping zone	Kelp patch	
	Center	Edge		Edge	Center
Spongia	0.22	—	—	0.65	6.70
Polychaeta	0.5(0.1)	0.2	0.01	0.01	0.02
Balanus algicola	0.01	0.2	1.99(0.5)	1.63(0.7)	0.03
Isopoda	0.01	0.01	0.01	—	0.01
Amphipoda	—	0.01	0.001	0.01	0.01
Callochiton castaneus	0.6(0.1)	0.1	2.27(1.2)	0.42(0.1)	1.65(0.4)
Patella sp.	—	—	16.5	12.0	—
Argobuccinum argus	104.1(26.3)	21.4	10.2	—	—
Thais squamosa	9.6	12.7(5.5)	—	—	8.6
Aulacomya ater	682.2(216.4)	432.2(180.3)	39.6(9.5)	66.0(13.2)	867.5(140.0)
Henricia ornata	—	0.2	—	—	8.7(2.9)
Patiria granifera	21.1(3.3)	19.6(4.9)	—	—	11.2(6.1)
Ophiotrix fragilis	10.4(4.2)	38.1(6.2)	0.01	—	3.0(0.7)
Parechinus angulosus	355.1(88.9)	328.5(72.0)	—	0.01	93.5(26.1)
Thyone aurea	1 088.1(358.9)	1 604.8(270.5)		0.01	588.5(192.0)
Pentacta doliolum	327.5(140.4)	2 017.0(180.3)	—	1.26	2 708(380.6)
Pyura stolonifera	—	—	—	—	1 193(109.3)
Rhodophyta	1.02(0.2)	0.5	0.21	2.6(1.7)	0.45(0.8)
Total (g/0.1 m^2)	5 546.52	4 475.52	70.81	84.60	5 490.87

followed the faster moving organisms, produced a complete coverage of the primary substrate. The original structure of the animal patch assemblage was reestablished only (Velimirov, in prep.) after the settlement of the filter feeding cucumbers within the experimental clearing. This was observed in all (n = 10) experimental clearings and shows that if place is available it will be occupied. This observation was true for all seasons.

Clearing of primary substrate at the edge of a kelp patch led to the following observations : the strip of bare rock between animal and kelp patch was populated in the same sequence as the experimental clearing in the animal patch. However, colonization of the clearing in the adjacent kelp patch was mainly achieved by *P. doliolum* and *T. aurea* which covered between 40 and 50 % of the kelp-free area. Other faunal components, like *P. angulosus*, *T. squamosa*, *Patiria granifera* and *Argobuccinum argus* (for others *see* Table) followed after the cucumbers were already established. The wedge-shaped coverage pattern of the animal layer was observed to be determined by the sweeping activity of the kelp plants at the edge of the experimental clearing (*see* Fig. 3). This wedge shaped coverage of the former sweeping zone and the cleared surface within the adjacent kelp bed was reached between 50 and 75 days. This configuration was maintained over a period of 7 months in 5 experimental sites.

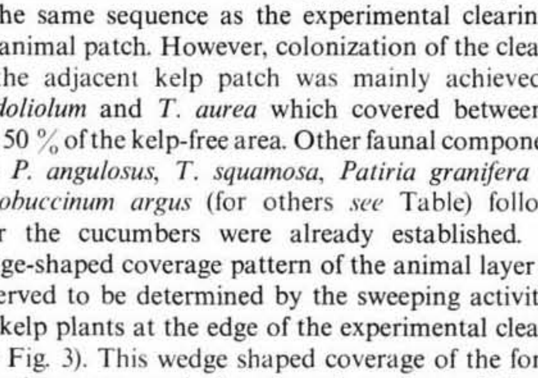

Figure 3

Sketch showing influence of kelp sweeping inhibiting faunal progression into kelp patch : a) experimental clearing ; b) experimental clearing 50 days later.

DISCUSSION

The species and biomass distribution in the different areas and the results of clearing experiments indicate that at the edge of these distinct kelp patches progression and regression processes take place. When an area of dense animal coverage is cleared, it is found that this area is subsequently colonized by kelp and finally the same components which have been outcompeted in earlier stages reappear in the established patch (Velimirov, in prep.).

A major problem in observing successions within communities is that a succession is only recognized as taking place, when the specific composition of the community is changing. It is defined as having stopped when the composition of the community is not changing. In many of the systems the time elapsed between these developmental stages surpasses the life time of the observer.

However, different stages of development can be recognized and ranked on a time scale. Observation of single plants, small expanding kelp patches and large established kelp patches lead to an understanding of the importance of sweeping in maintaining a predator-free zone, promoting the settlement of kelp-sporophytes by sweeping protection in the swept area (Velimirov, Griffiths, 1979) with some reservations. Among the few grazers (Velimirov *et al.*, 1977 ; Field *et al.*, 1980) which represent a potential threat for the kelp patch only two mollusc species can move across the sweeping boundary and are regularly found in the kelp bed. *Haliotis middae*, in low density at the study site, was mainly recorded by line transect counts (Velimirov *et al.*, 1977) and can trap kelp fronds underfoot to feed on them. Kelp sweeping is therefore advantageous to its feeding mode since the rythmic movement of the fronds increases the probability of the encounter between mollusc and prey. Additionally the adhesion force of *H. middae* make removal by sweeping kelp impossible.

The other species, *Patella* sp. and *Patella tabularis*, smaller in weight and size, feed preferentially on smaller algae and fresh sporophytes. Again the thick shell and adhesiv force of *Patella* sp. allow them to withstand the removal by sweeping and as in *H. middae* the density of *Patella* sp. is low.

Comparatively high densities are noted in the animal patches for *Parechinus angulosus* which is a potential grazer. This species is classified as a herbivore according to Ott (1981), since it mainly consumes kelp debris, defined as live or dead material being no longer active in maintenance and propagation of the stand (Velimirov *et al.*, 1981).

The constant wave-induced sweeping of kelp fronds inhibit predation on sporophytes and penetration into the patches. A destructive influx of sea urchins, as repeatedly reported from other kelp beds (Breen, Mann, 1976; Miller, Mann, 1973; Mann, 1977; Foreman, 1977) was never observed in South African kelp beds.

Of the two sedentary species which can withstand sweeping and are regularly found in the sweeping zone (Table). *Aulacomya ater* is the dominant species and influences the expansion rate of the kelp bed as well as the distribution of the faunal components in the different areas, the mussel-bed creating a new type of cavernous hard substrate.

During 5 years of studies on the energetics of the system, kelp was often observed to grow on *Aulacomya*. Kelp bed expansion may be retarded but not stopped by encountering an *Aulacomya* settlement in the sweeping zone. The overgrowth of *Aulacomya* by sporophytes thus leads to inclusion of the mussel-bed within the kelp patch. With this integration all faunal components living between the mussels (mainly urchins, molluscs and cucumbers) are now sheltered from sweeping and can penetrate the kelp patch where they can move freely.

CONCLUSION

Three possibilities exist for faunal components to penetrate into an established kelp patch : *a*) by larval input or dispersion of early stages of development by water movement; *b*) by living within musselbeds which become overgrown during expansion of a kelp patch; *c*) by water movement during periods of storm, uprooting kelp plants and clearing a large enough area to allow the animals to occupy the substrate and expand without being swept away.

A model of the mechanisms that would bring about a successional change at the edge of a kelp patch, leading to its expansion or to its suppression is represented in Figure 4. It can be seen that the unidirectional development of a succession, made possible by sweeping, can be retarded when a musselbed is encountered, leading to a limited progression of the faunal components into the kelp patch. Drastic changes which increase predation pressure and competition within the patch so that an animal patch may get established are only brought about by storms. Wave action can produce large and deep clearing at the edges of the stands, and allow invasion of the faunal components so that unprotected sporophytes within the kelp patch are preyed upon. Since grazing animals live within the kelp bed on the substrate and in hold-fasts, the input of new grazers could lead to the deterioration of parts of the kelp patch.

The model displays two relatively stable points, the kelp patch and the animal patch, and a loop system reinforcing the stability of the one or the other point. However, in this extremely simplified model more loops lead to the established kelp patch than to the animal patch and one wonders whether this corresponds to reality. In more than five years of observation during which edges of kelp patches were under study, expansion

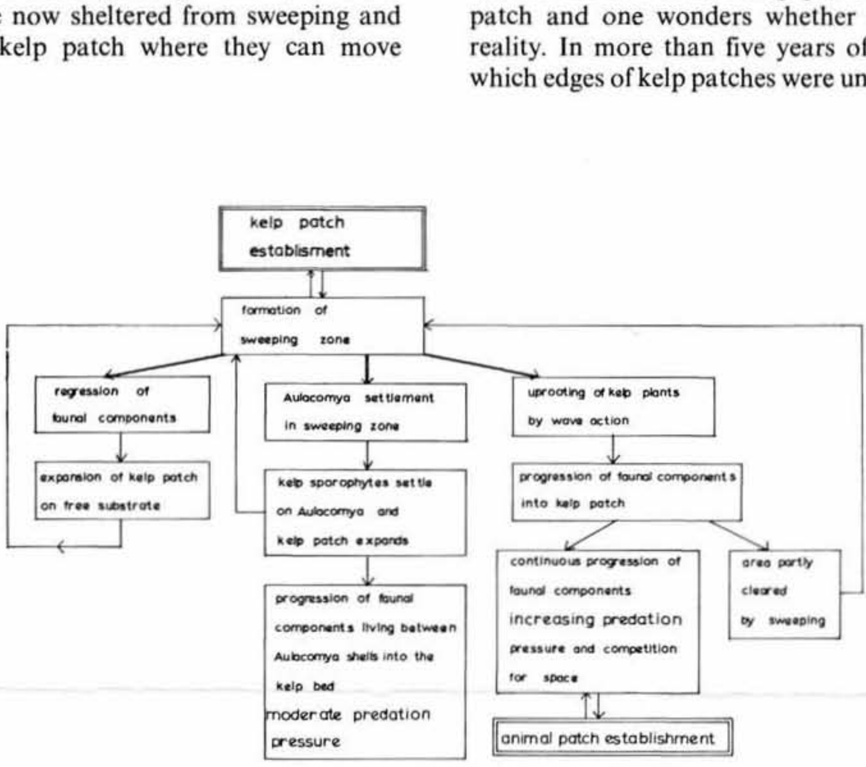

Figure 4

Model describing the mechanisms leading to the expansion or destruction of a kelp patch.

was only observed in very small patches. On average large patches lost most of the substrate which they took over whereas destruction of the edges during storms and subsequent progression of animals had more lasting effects. And yet, in none of the storm-induced invasions of the kelp patch grazers, herbivores and filter feeders was a destruction of a kelp patch observed.

In the case of small kelp patches the succession induced by frond sweeping is closely correlated with an expansion of this kelp patch. With increasing size of the patch, however, this mechanism seems to be more important in its function as a repair mechanism when invasion of faunal components takes place after edge destruction during storm periods.

Acknowledgements

I thank Pr. M. Mizarro and B. Höller for drawing the figures and M. Triebl for typing the manuscript.

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